A new pedunculate barnacle (Cirripedia: Heteralepadidae) from the Northwest Atlantic

L. Buhl-Mortensen and W. A. Newman

(LB-M) Benthic Habitat Research Group, Institute of Marine Research, P.B. 1870 Nordnes N-5817 Bergen, Norway, e-mail: lene.buhl-mortensen@imr.no; (WAN) Marine Biological Research Division, Scripps Institution of Oceanography, La Jolla, California 92093-0202, U.S.A.

Abstract.—A species of Heteralepas has been discovered attached to a gorgonian coral from 500 meters of depth off Nova Scotia (~42^a N). A brief review of the previously described Heteralepas species is presented. Of the 29 previously described species (including 2 in synonymy), the new species is more similar to some from the Indo-West Pacific than to any of the 8 previously known species from the Atlantic. While the new species can be distinguished from Atlantic but not some Pacific species by some characters, it can be distinguished from all species of the genus by small but marked differences in the configuration of the apertural region of the capitulum. Therefore it is proposed as a new species, Heteralepas cantelli, the most northern known member of the family.

Introduction

A specimen of *Heteralepas* was discovered during a survey of the coral-associated fauna at ~42°N on the continental shelf and slope off Nova Scotia, Canada, in 2002. This is not only several degrees of latitude farther north than any previously known species of the genus along the Atlantic seaboard, but at a higher latitude than any previously known species of *Heteralepas* (Young 1999, Zevina 1982). It was collected by a benthic trawl from ~500 m of depth, attached to the gorgonian *Primnoa resedaeformis* (Gunnerus, 1763).

Thirty species of Heteralepas have been described, and 2 of these are presently in synonymy. Of the 28 recognized species (Table 1), 8 have been recorded from the Atlantic; 3 from the Western Atlantic, and 1 found in both areas; H. cornuta (Darwin, 1852), H. lankesteri (Gruvel, 1901), H. belli (Gruvel, 1901), and H. luridas (Zevina, 1975), and H. microstoma (Gruvel, 1901), H. meteo-

rensis Carriol, 1998. H. alboplaculus Zevina & Kolbasov, 2000 and H. segonzaci
Young, 2001 plus H. cornuta respectively
(Zevina 1975, Young 2001). All these species are from relatively low latitudes and
none compare favorably with the new form.
The closest affinities of the new form are
with species like H. japonica (Aurivillius,
1892) from the Indo-West Pacific. However,
the new form can be distinguished from all
previously described species by characteristics of the apertural regions, and therefore
it is considered to represent a new species.

Systematics

Subclass Cirripedia Burmeister, 1834 Superorder Thoracica Darwin, 1854 Order Pedunculata Lamarck, 1818 Suborder Heteralepadomorpha Newman, 1987 Family Heteralepadidae Nilsson-Cantell, 1921

Pilsbry (1907b) revised Alepas and extracted two distinct but related taxa from it,

Table 1.—Species of the genus Heteralepas of the world ocean from locality and depth data compiled from Foster (1979), Ren (1983), Carriol (1998), Zevina & Kolbasov (2000) and Young (2001), ? = taxonomic uncertainty (see discussion), * = species that are compared with H. cantelli sp. nov. because of similarity in external morphology and/or geography.

Heteralepas	Western Atlantic	Eastern Atlantic	Eastern Pacific	Indo-West Pacific	Depth (m)
1 H. comuta (Darwin, 1852)	West Indies, North Carolina to Brazil	W. Africa & offshore islands to Madeira, Meteor Seamount	?Chile	Andaman Sea, Phillippines	73–210
2 H. japonica (Aurivillius, 1892)	ı	ı	1	Japan to New Zealand and west to Re-	48-1,020
= H. indica (Gravel, 1901)				Phillippines, Australia, New Zealand	
3 ?H. quadrata (Aurivillius, 1894) = H nermonicola (Hiro 1937)	ı	1	N. & S. America	Japan, New Zealand	Shallow water
4* H. lankesteri (Gruvel, 1900)	West Indies, Brazil	1	1	I	91-1.500
5* H. belli (Gruvel, 1901)	Cuba	I	1	ı	. 6-
6* H. microstoma (Gruvel), 1901)	1	Azores, Madeira, Mete-	1	1	269-623
		or Seamount			
7 H. gigas (Annandale, 1905)	1	-	1	Bali Straits	238-915
8 ?H. malaysiana (Annandale, 1905)	1	1	1	Malaysia	54
9 H. ovalis (Hoek, 1907)	[1	1	Malaysia	984
) H. tenuis (Hoek, 1907)	1	1	ı	Malaysia	204
 H. rex (Pilsbry, 1907a) 	1	1	1	Hawaiian Islands	415-428
2 H. cygnus Pilsbry, 1907b	1	1	?California	1	3
3 H. nicobarica Annandale, 1909	1	1	1	Nicobar Islands	ż
4 H. vetula Pilsbry, 1911	1	1	1	Japan	277-329
5 H. ?dubia Broch, 1922	1	1	1	New Zealand	55-73
5 H. hatai Hiro, 1937	1	1	1	Japan	Intertidal
	1	1	1	Tasmania	450
	1	1	S.E. Pacific	1	228
	Caribbean	1	1	1	300-700
	1	1	1	Japan	400
	1	1	S.E. Pacific	. [300
	1	1	1	China Sea	217
24 H. fessa Zevina & Shcreider, 1992	I	1	1	N. of Madagascar	480
	1	Meteor Seamount	1		300
26 H. ?alboplaculus Zevina & Kolbasov, 2000	1	Meteor Seamount	1	1	280-300
	1	Meteor Seamount	1	1	2,235
28 H. cantelli sp. nov.	Nova Scotia	ı	1	1	200

Heteralepas and Paralepas, but he left them in the family Lepadidae. Nilsson-Cantell (1921) noted that these two genera, in addition to lacking calcareous plates, differed from the remaining Lepadidae in the nature of their trophi and cirri and therefore he proposed a new family, the Heteralepadidae, for them. Species of Heteralepas are generally considered to have ctenopod or lasioned cirri used for setose feeding, while those of Paralepas have acanthopod cirri, generally used to feed on the food or tissues of their hosts, including the eggs of hosts such as spiny lobsters. The two genera are further distinguished by the inner ramus of the posterior two pairs of cirri (cirri V & VI) being similar to the outer rami in Paralepas, but conspicuously reduced in length and breadth in Heteralepas. However, as will be noted in the discussion, there is at least one species that is somewhat intermediate in these characters and it likely should be assigned a genus of its own.

Heteralepas Pilsbry 1907b Heteralepas cantelli sp. nov. (Figs. 1–4)

Type material.—The sole specimen (holotype) is deposited in the National Museum of Washington, Washington, D.C. USNM 1019509.

Etymology.—Named in honor of the Swedish cirripedologist, Carl August Nilsson-Cantell (cf. Newman 1990) who erected the family Heteralepadidae.

Material.—Known from a single specimen collected in the Northeast Channel, south of Nova Scotia, Canada (41°55.9'N, 65°42.5'W), by a commercial bottom trawler on October 9, 2002 from 500 m depth. It was attached to the exposed skeleton of the gorgonian Primnoa resedaeformis.

Diagnosis: Capitulum and peduncle relatively smooth, without tubercles, carinal ridge or indications of the insertions of the carapace adductor muscle; apertural region slightly recessed or depressed below general surface; aperture ~ ½ height of the ca-

pitulum, with crenulate lips restricted to upper 1/3.

Description

The fresh specimen was translucent vellowish pink. The capitulum is 3 cm high and 2 cm wide, globular or nearly ovoid in lateral aspect, slightly pointed apically, laterally compressed, frontal margin interrupted by a depressed apertural region with slightly protuberant lips in the upper 1/3 of the aperture (Figs. 1A, B, 2A, B). The slightly recessed apertural region is outlined by a thin edge and in the region below it, where the carapace adductor muscle is found, there is a chin-like thickening. Otherwise the capitulum is smooth, without carinal crest or ridge, warts, bumps or protuberances. Aperture 1/2 height of capitulum; crenate lips produced in upper 1/3. Peduncle 1.2 cm in diameter, equal in length to capitulum and marked with several folds and lines in the otherwise smooth cuticle, basal portion expanded into attachment disc. Labrum too damaged to describe; mandible (Fig. 3B) with 4 teeth including inferior angle, surface covered with numerous fine setae, lower margins of teeth 1-3 with a few fine pectinations (5 under the first and second, and 3 under the third tooth; Fig. 3B, a1-a3), First maxilla (Fig. 3C) with cutting edge stepped (plane of superior cutting edge indented relative to plane of inferior cutting edge) rather than notched, with three major spines (one large flanked by two somewhat smaller ones) above and approximately 14 spines below step, with soft setae in a group along the superior margin and spread out along the inferior margin, lateral surfaces clothed with numerous setae. Second maxilla (Fig. 3A) with a proximal cluster of long spine-like setae and a similar array of setae separated into two groups along the cutting edge. Cirrus I not separated from posterior

Cirrus I not separated from posterior pairs but modified as a maxilliped of relatively short, unequal, densely setose rami; cirri II–VI basically similar in structure, se-

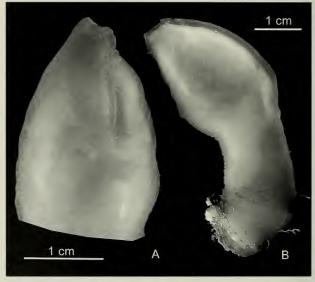


Fig. 1. Heteralepas cantelli sp. nov.: A, right-frontal aspect of capitulum, enlarged to show details of apertural region; B, lateral aspect of entire animal;

tation lasiopod (Fig. 4C). However, while cirri II–IV have long subequal rami nearly equal in length to the outer rami of cirri V and VI, the inner rami of V and VI are atrophied (Fig. 4D, Table 2). The number of articles comprising the cirri is as follows:

Cirrus: I II III IV V VI Inner ramus: 18 42 56 56 25 22 Outer ramus: 24 51 57 58 60 60

Caudal appendage (Fig. 4D) of 13 articles, slightly longer than pedicel of cirrus VI. Penis (Fig. 4A, B) relatively long, slender, annulated, without specialized hooks or grap-

ples but clothed with numerous, long soft setae distally.

Discussion: The cirri of the new species are fully lasiopod (Fig. 4C) and the inner rami of the cirri V & VI are substantially reduced in length as well as breadth (Fig. 4D; Table 2). Therefore the new species is a Heteralepas in the strict sense. The number of articles comprising the rami of the cirri and the form of the mouthparts, while sometimes useful in distinguishing species, are considered somewhat variable (Nilsson-Cantell 1921), as are elaborations of the capitulum as well as its length relative to the peduncle (Young 2001). Therefore keys,

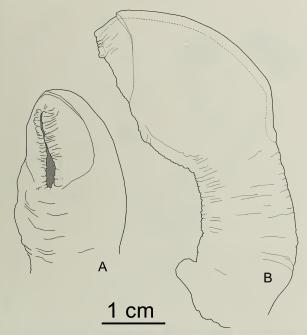


Fig. 2. Heteralepas cantelli sp. nov.: A, left-frontal aspect of capitulum, enlarged to show details of apertural region; B, lateral aspect;

such as that presented by Zevina (1982) for the 19 species of *Heteralepas* recognized at the time, should be used with caution.

Zevina (1982) did not include complete synonymies in her monograph, and at least two species once attributed to Heteralepas were assigned to Paralepas without amending either genus. Therefore we review all species attributed to the genus and, as can be seen from Table 1, 28 species (including the new form) are presently recognized. In

the process we encountered some problematic forms, and these are briefly discussed below before moving on to those that are strictly relevant to the new species.

Heteralepas quadrata (Aurivillius, 1892). This shallow-water species [including 1) H. percnonicola as a junior synonym (Hiro 1937), 2) the forms attributed to the species by Rosell (1972), and 3) a little-known form from the Eastern Pacific (Zullo 1991) sat uncomfortably in Heteralepas un-

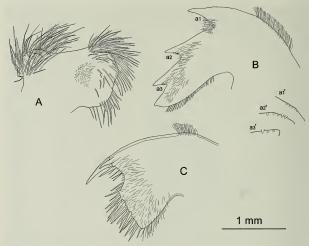


Fig. 3. Heteralepas cantelli sp. nov., mouth parts: A, second maxilla; B, mandible (a1'-a3', enlarged undersides of teeth a1-a3); C, first maxilla. (A-C same scale).

til Foster (1979) transferred it to Paralepas. a decision accepted by Zevina (1982). However, the species also sits uncomfortably in Paralepas because in some ways it is morphologically intermediate between the two genera. The characters largely involve the cirri, their setation being neither strictly lasiopod nor acanthopod, the relatively low number of articles of their rami, and the somewhat reduced inner rami of cirri V & VI, as well as the somewhat intermediate armature of the mandible and first maxilla. This suggests that proposal of a new genus is in order, and such a study would be of interest to evolutionary biologists as well as cirripedologists in light of the inferred relative primitiveness of the Heteralepadidae (Foster 1979), a view recently corroborated genetically and morphologically (Harris et al. 2000; Pérez-Losada et al. 2004). While there are a number of samples from the Eastern Pacific attributed to this species in the Benthic Invertebrate Collection at Scripps Institution of Oceanography, an appropriate review of the situation would also require studying materials from the Western Pacific. However, such a study is beyond the scope of the present paper.

**PHEEPalepas malaysiana (Annandale, 1905). From a telegraph cable at approximately 54 m depth in the Gaspar Straits. Annandale (1909:84) accepted Pilsbry's (1907b) revision of Alepas and transferred Alepas xenophorae Annandale, 1906 to Heteralepas (Paralepas) and described Heteralepas (Heteralepas) nicobarica sp. nov. In the same paper, in a list of species

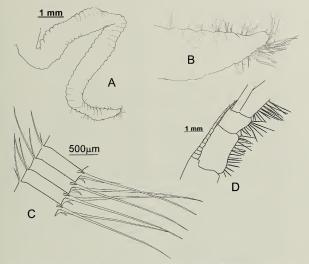


Fig. 4. Heteralepas cantelli sp. nov., thoracic appendages: A, penis; B, enlargement of distal portion of penis; C, intermediate segments of outer ramus of cirrus VI; D, posterior of thorax supporting right caudal appendage and pedicel of cirrus VI with proximal portions of inner and outer rami in outline (narrow and wide respectively, boundaries of articles omitted).

contained in the Indian Museum, Annan-dale (1909:130) included Heteralepas ma-layana (sic) under the subgenus Heteralepas. This was presumably because Annan-dale (1905:81) had clearly stated that the posterior (= inner) ramus of cirrus V was "... reduced to a mere thread, less than one-third as long as the anterior ramus", and that cirrus VI was "... in much the same condition". However, subsequently, and without a word of explanation, he (Annandale 1916:298) transferred Heteralepas malaysiana to the subgenus Paralepas. While Newman (1960) retained malaysiana in Heteralepas s.s., Zevina (1982) followed

Annandale by returning it to Paralepas. This is puzzling, considering the habitat as well as the characteristics of cirrus V & VI given in the original description. In light of these considerations, and the fact that the ornamentation of the capitulum appears more similar to that of Heteralepas rex (Pilsbry, 1907a) from Hawaii and H. utinomii Newman, 1960 from Tasmania than it does to any species of Paralepas, we have tentatively returned the species to Heteralepas.

?Heteralepas ovalis (Hoek, 1907): This species is represented by a single specimen taken along with *Paralepas morula* from an

Table 2.—Morphological comparison among Heteralepas japonica, H. microstoma, H. meteorensis, H. belli, H. lankesteri and H. cantelli sp. nov., based on C/P Ratio of length of capitulum (C) to length of peduncle (P). A/C = Ratio of height of aperture (A) to height of capitulum (C).

		n. saponea	ii. macrostoma	r. mercorensis	n. oenn	H. lankesteri	er, cantent sp. nov.
Demarcation between capitu-		Varying	Weak	Weak	Clear	Clear	Weak
Width of capitulum to capitu- lo-peduncular junction		Varying	Slightly wider	Slightly wider	Wider	Wider	Slightly wider carinal side
Capitulum	Width (cm)	0.6-2.3 (1.5)	2.3	1.2-1.7	2.5	1.2-2.0	2
	Length (cm)	0.9-3.6 (2.0)	1.7	1.2-1.8	1.6	1.7-2.2	3
Peduncle	Width (cm)	0.5-1.9 (0.9)	6.0	0.7-1.3	0.95	0.9-1.3	1.2
	Length (cm)	0.5-11.6 (3.8)	2.4	3.1-7.2	3.2	1.3-3.8	3
	C/P	0.2-1.8 (0.5)	0.7	0.25-0.47	0.5	0.6-1.3	1.0
Mantle	**Chitinous tubercles present	No	Yes	6.	Yes	Yes	No
Carinal margin thickened		Varying	Yes	Yes	Yes	Yes	No
Aperture	A/C	1/2	1/2.5	14-16	77	3%	77
	Flaring from side	No	No?	No	Yes	Yes	Partly
	Crenulate	5	6	Slightly	No No	Conspicuously	Slightly
	Lower margin demarcated	6	6	6.	No	Yes	No
	Tubular	No	Yes	3	?Yes	?Yes	No
Cirrus V Articles	Inner ramus	13-29	29	23	27	19-21	25
	Outer ramus	36-69	6.	93	٥.	74-92	09
Cirrus VI Articles	Inner ramus	13-27	56	26	27	19-22	22
	Outer ramus	37-68	6.	92	٥.	68	09
	Caudal appendage	4-12	15	41	5	10-12	13
Mouth parts	Mandible pectination	* *	Yes	Yes	Yes	No	Yes

* = considered synonymous by Young (2001).

^{** =} Refers to special vase-shaped structures "de granulations chitineuses arrondies dont quelque-unes portent des crochets" (Gruvel 1902). *** (for H. japonica) = see Discussion.

echinoid spine in Malaysian waters. Hiro (1936:223) noted that nothing is known of the internal parts, but from the original figures it is evident that the capitulum to aperture ratio is approximately 3:1. This is suggestive of *Paralepas*, but for lack of more conclusive evidence we have left it in *Heteralepas*.

Heteralepas cygnus Pilsbry, 1907b: The original description was based on a specimen acquired from the "Ward's Natural Science Establishment, Monterey, California", and hence the specimen was presumably from California, but it has not been recorded from this region since. Furthermore, Annandale (1909) indicated that there is a specimen in the Edinburgh Museum, questionably from the West Indies. The description may be adequate to distinguish it from similar albeit relatively undistinguished forms, but what ocean it came from remains uncertain.

Heteralepas cornuta (Darwin, 1852): A species usually having more-or-less distinctive carinal protuberances on its capitulum. first reported from the Caribbean (presumably from 90 m or so). It has since turned up in the Gulf of Mexico (Gittings et al. 1986), off Madeira and other West African islands (cf. Haroun et al. 2003), and along the coast of Northwest Africa, Furthermore it has been found in the Indian Ocean, the Philippines and the Southeast Pacific, off Chile (4315 m!) (cf. Young 2001 for review). Young (2001) commented not only on its wide geographical range and the extraordinary depth of the Chilean record compared to other populations attributed to the species, but on differences in cirral setation of the Chilean form compared to the population he has studied from the eastern Atlantic. Thus H. cornuta may represent a number of similar species. In any event, like the previous species, it is sufficiently distinct from the new form to no longer concern us here.

Heteralepas microstoma (Gruvel, 1901): Known from off Madeira, the Azores and Meteor Seamount immediately to the south. While known to range from between 269-623 m, it is most commonly found around 300 m (Young 2001). Zevina & Kolbasov (2000) illustrated and compared it to another recently described species, H. meteorensis Carriol, 1998, as well as to their new species, H. alboplaculus Zevina & Kolbasov, 2000, which was also from Meteor Seamount, Having such similar forms sympatric on Meteor Seamount, and then largely from the same depth, is troubling. Young (2001) synonymized H. meteorensis with H. microstoma, but he was apparently unaware of the work of Zevina & Kolbasov (2000) who claimed that all three species can be distinguished from each other by minute cuticular structures revealed by SEM. However, their photographs are not clear in this regard. As can be seen from our Table 2, there appears to be little in the way of macro-morphological differences among them, although the peduncle of H. meteorensis seems to be relatively longer and the aperture does not appear as tubular as in H. microstoma. On the other hand, Heteralepas alboplaculus is described as having the capitulum and to some extent the peduncle covered by well-spaced tubercles containing calcareous structures. Such calcareous structures are unprecedented in the family and could be the work of a pathogen. We hope that workers in the Atlantic will clarify this situation in the near future. In the meantime, while the specific status of H. meteorensis and H. alboplaculus is uncertain (Table 1), we have included the former as well as H. microstoma in Table 2 for comparative purposes.

When it comes to determining the affinities of the new species, the logical place to begin is in the Atlantic. Of the 8 previously known species of *Heteralepas* noted in the introduction, 5 occur in the eastern Atlantic. These include *H. cornuta*, alboplaculus and segonzaci, and taking their capitular features at face value, they are distinct from the new form and therefore no longer concern us here. This leaves *H. microstoma* and meteorensis, which are very similar if

not synonymous, but as noted above both have been characterized in Table 2 for comparative purposes.

As for the western Atlantic species, H. cornuta, which ranges as far north as the Carolinas, was noted above as being distinct from the new form. This leaves H. luridas, belli and lankesteri. The first, from 300-700 m of depth in the Caribbean, is known to range between 2 and 9.5 mm in height and the specimen illustrated in the original description is less than 6 mm high. so it is a small species. Its capitulum, with a somewhat tubular or flaring apertural region, is otherwise undistinguished, and its cirral and caudal appendage counts are lower than in the new species. So, assuming H. luridas is not based on juveniles, it too need no longer concern us. This leaves H. belli and lankesteri, and since in outward appearance they are similar to the new form, they have been included in Table 2. As we shall see, so far none of the species included in Table 2 agree well with the new species in numerous detail; but what about species from the Indo-Pacific?

Of the Indo-West Pacific species, H. japonica and similar species such as H. fulva from the Southeast Pacific are rather close to the new form. The former has been reported from between 18 and 1020 m depth from Japan to Singapore, Australia and New Zealand, the Nicobars in the Andaman Sea and Réunion Is. (Foster & Buckeridge 1995). Therefore, while not as wide-ranging as H. quadrata, it is wide-ranging compared to most species of the genus. Part of this range is due to synonymies, and that of Nilsson-Cantell's (1927, 1938) for H. indica (Gruvel, 1901) has long been accepted. This extended the range of the species to Singapore and into the Indian Ocean where it was reported from Nicobar Is, on floating wood. Furthermore, Foster (1979), in his report on New Zealand cirripeds, synonymized H. dubia Broch, 1922 from 55-72 m in Disaster Bay, Australia, with H. japonica. However, Zevina (1982), without explanation, continued to recognize H. dubia as a distinct species, and subsequent authors have followed suit.

Considerable variability in characters might be expected in such a wide-ranging species and for present purposes we are accepting the opinion of these authors. However, considering such variation in cirripeds as geographical rather than indicative of genetically distinct populations has generally proven wrong (Newman 1993). Thus caution seems in order because the reported variations in the mandible of presumed H. japonica from different populations, appear to go beyond the range of variability found within a species. Although Aurivillius (1894) did not illustrate the mandible of H. japonica, his written description agrees with Nilsson-Cantell's (1921:247, fig. 43b) and Pilsbry's (1911:71, fig. 4A) illustrations, and also with that of Gruvel (1902: 284, Pl. 24, fig. 24) for H. indica. Thus the teeth of the mandible appear to be without pectinations, but on close inspection of Nilsson-Cantell's illustration there might have been low pectinations of the lower margins of teeth 1-3, especially 2 and 3. However, since there is no such suggestion in the other illustrations, the evidence favors the mandible being simple.

The situation at the southern end of the range for H. japonica looks quite different with regard to the mandible. Foster (1979) synonymized H. dubia Broch from Australia, and the population he was studying in New Zealand, with H. japonica. While Broch (1922:288, fig. 37B) gave no indication of pectinations on the first tooth, he clearly illustrated them on the upper sides of teeth 2-4 as well as the lower sides of 2 and 3. Foster (1979:16, fig. 3J) illustrated the same for the upper sides, but limited pectinations on the underside to tooth 1. So. the populations attributed to this species from north and south of the equator appear to differ in the characteristics of the mandible, and the new species, with its inconspicuous pectinations on the lower sides of teeth 1-3 (Fig. 3, a1-a3), differs from both of them.

In view of the foregoing considerations we include *H. dubia* in Table 1 as a questionable species rather than a synonym of *H. japonica*. Nonetheless, *H. japonica* still includes sufficient variability to make it an ideal Indo-Pacific representative similar to the new form from the Atlantic, and therefore it is included in Table 2 for comparative purposes.

Summary and Conclusions

The essentially naked heteralepadids present a difficult problem to systematists since, being unarmored, they lack a number of distinct features customarily utilized in separating genera and species (Zullo & Newman 1964). Aside from the work of Nilsson-Cantell (1921, 1927), and to some extent, Young (2001), no studies have evaluated the usefulness of morphological characters in distinguishing Heteralepas species. Thus it is difficult to establish a new species with a high degree of certainty. But, in spite of the latitude allowed by synonymy, the present form could not be assigned to any known species.

As can be observed in Table 2, the Atlantic species most similar to the new species (H. microstoma, meteorensis, belli and lankesteri) are readily distinguished from it as well as from H. japonica from the Indo-West Pacific, by several characters, However, the new species, H. cantelli, cannot be distinguished from H. japonica by the characters presented in the table. This is due in part to the variability attributed to H. japonica, but there are notable differences between these two species, not included in the table, that distinguish them. These include 1) the lack of any indication of a carinal thickening, crest, or protuberances along the carinal margin (but sometimes also found lacking in individuals of H. japonica), 2) a marked crenation of the apertural margin largely restricted to the upper third rather than along its entire margin, and 3) a slightly depressed area around the entire apertural region, setting it off from the general surface of the capitulum. The last two differences are sufficient not only to distinguish the new form from *H. japonica*, but from all known heteralepadids.

Acknowledgments

We thank Paulo S. Young, Museu Nacional/UFRJ, Rio de Janeiro, Brazil, who died tragically before the publication of this paper, for advice on the Atlantic species during preparation of the manuscript, and Pål B. Mortensen, Bedford Institute of Oceanography, Dartmouth, Canada and Vladimir E. Kostylev, Natural Resources Canada, Dartmouth, Canada, for helping with the translation of publications in German and Russian, respectively. While we would also like to thank two judicious referees (John S. Buckeridge, EOS, Auckland University of Technology, as well as Paulo S. Young) for reviewing the manuscript, we are solely responsible for any errors that remain.

Literature Cited

Annandale, N. 1905. Malaysian barnacles in the Indian Museum, with a list of Indian Pedunculata.— Memoirs of the Asiatic Society of Bengal 1(5): 73-84.

—. 1906. Preliminary report on the Indian stalked barnacles.—Annals and Magazine of Natural History 17(7):389–400.

—. 1909. An account of the Indian Cirripedia Pedunculata, part 1.—Family Lepadidae (s.s.). Memoirs of the Indian Museum 2:61–137.

—. 1916. Barnacles from deep-sea telegraph cables in the Malay Archipelago.—Journal of the Straits Branch of the Royal Asiatic Society 74: 281–302 + pls. IV–VI.

Aurivillius, C. W. S. 1892. Neue Cirripeden aus dem Atlantischen, Indischen und Stillen Ocean.— Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, Stockholm 3:123–134.

—. 1894. Studien über Cirripeden. Kongliga Svenska VetenskapsAkademiens Handlingar,— Uppsala 26(7):5–107 + 9 pls. 1–9.

Broch, H. 1922. Studies on Pacific cirripeds. Pp. 215–358 in Paper from Dr. Th. Mortensen's Pacific Expedition 1914–1916. X. Videnskabelige meddelelser fra Dansk Naturhistorisk Forening i Köbenhavn 73. Carriol, R. P. 1998. A new pedunculate cirriped (Thoracica, Heteralepas)

- from the northeast Atlantic Ocean.—Zoosystema 20(3):505-509.
- Darwin, C. R. 1852. A monograph on the sub-class Cirripedia, with figures of all the species. The Lepadidae; or, pedunculated cirripedes. Pp. 1– 400 + pls. 1–10. Ray Society, London (1851).
- Foster, B. A. 1979. The Marine Fauna of New Zealand; Barnacles (Cirripedia: Thoracica).—New Zealand Oceanographic Institute Memoir 69:1–159 (1978).
- ——, & J. S. Buckeridge. 1995. Barnacles (Cirripedia, Thoracica) of seas off Réunion Island and the East Indies.—Bulletin du Muséum national d'Histoire naturelle, Paris, 4° séries, 16(2-4):345-382.
- Gittings, S. R., G. D. Dennis, & H. W. Harry. 1986. Annotated guide to the barnacles of the northern Gulf of Mexico. Sea Grant College Program, Texas A & M University, College Station, 36 pp.
- Gruvel, A. 1900. On a new species of the genus Alepas (A. lankesterl), in the collection of the British Museum.—The Annals and Magazine of Natural History. Ser. VII, 6:195–199 + pl.VIII.
- ——. 1901. Diagnoses de quelques espèces nouvelles de Cirrhipèdes.—Bulletin, Muséum national d'Histoire naturelle, Paris 7:256–263.
- ——. 1902. Sur quelques Lépadides nouveaux de la collection du British Museum.—Transactions of the Linnean Society, London, Second Series, 8: 277-294 + Pl. 24.
- Haroun, R., R. H. Pérez, & P. D. Santana. 2003. Cirripedia. Pp. 67–68 in L. M. Abad, J. L. M. Esquivel, M. J. G. Sanahuja and I. J. Zamorna. eds., Lista de especies Marinas de Canarias (Algas, Hongos, Plantas y Animales). Consejeria de Politica Territorial y Medio Ambiente del Gobierno de Canarias, Tenerife, 200 pa.
- Harris, D. J., L. S. Maxson, L. F. Braithwaite, & K. A. Crandall. 2000. Phylogeny of the thoracican barnacles based on 18S rDNA sequences.— Journal of Crustacean Biology 20(2):393–398.
- Hiro, F. 1936. Descriptions of three new species of Cirripedia from Japan.—Bulletin of the Biogeographical Society of Japan 6(23):221–230.
- ——. 1937. Studies on Cirripedian fauna of Japan. II. Cirripeds found in the vicinity of the Seto Marine Biological Laboratory.—Memoirs of the College of Science, Kyoto Imperial University, Series B 12(3):385–478.
- Hoek, P. C. C. 1907. The cirripedia of the Siboga Expidition,—Pedunculata. Siboga-Expeditie 31a: 1–127.
- Newman, W. A. 1960. Five pedunculate cirripeds from the Western Pacific, including two new forms.—Crustaceana 1(2):100–116.
- . 1990. Carl August Nilsson-Cantell, 28 December 1893–14 January 1987.—Crustaceana 59(3):289–294.

- ——. 1993. Darwin and cirripedology. Pp. 349–434 in J. Truesdale, ed., The history of carcinology.—Crustacean Issues 8. Balkema, Rotterdam.
- Nilsson-Cantell, C. A. 1921. Cirripeden Studien. Zur Kenntnis der Biologie, Anatomie und Systematik dieser Gruppe.—Zoologiska Bidrag, Uppsala 7:75–390.
 - ——. 1927. Some barnacles in the British Museum (Nat. Hist.).—Proceedings of the Zoological Society of London 1927(3):743–790, figs. 1–19,
 - . 1938. Cirripedes from the Indian Ocean in the collection of the Indian Museum, Calcutta.—
 Memoirs of the Indian Museum 13(1):1–81 + pls. 1–3.
- Perez-Losada, M. J., J. T. Hoeg, & K. A. Crandall. 2004. Unraveling the evolutionary radiation of the thoracican barnacles using molecular and morphological evidence: a comparison of several divergence time estimation approaches.— Systematic Biology 53(2):244–264.
 - Pilsbry, H. A. 1907a. Hawaiian Cirripedia.—Bulletin of the Bureau of Fisheries 26:181–190 + pls. IV & V (1906).
 - ——. 1907b. The barnacles (Cirripedia) contained in the collections of the U.S. National Museum.—Bulletin of the United States National Museum 60:1–122 + pls. 1–11.
 - ——. 1911. Barnacles of Japan and Bering Sea.— Bulletin of the Bureau of Commercial Fisheries 29:61–84 + pls. VIII-XVII (1909).
 - Ren, X. 1983. Five new species of suborder Lepadomorpha (Cirripedia Thoracica) from Chinese waters.—Oceanologia et Limnologia Sinica 14(1):74-87.
 - Rosell, N. C. 1972. Some barnacles (Cirripedia Thoracica) of Puerto Galera found in the vicinity of the U.P. Marine Biological Laboratory.—National and Applied Science Bulletin 24(4):104– 283.
- Young, P. S. 1999. The Cirripedia (Crustacea) collected by the "Fisheries Steamer Meteor" in the Eastern Atlantic.—Arquivos do Museu Nacional, Rio de Janeiro 58:1–54 (1998).
 - —. 2001. Deep-sea Cirripedia Thoracica (Crustacea) from the northeast Atlantic collected by French expeditions.—Zoosystema 23(4):705—756.
- Zevina, G. B. 1975. Cirripedia Thoracica of the American Mediterranean.—Trudy Instituta Okeanologii 100:233–258 (in Russian).
 - . 1982. Barnacles of the suborder Lepadomorpha of the world ocean. II. Pp. 1–222 in Fauna U.S.S.R., Zoological Institute, Russian Academy of Science, Leningrad, 133 (in Russian).
- ——, & G. A. Kolbasov. 2000. Barnacles of the genus *Heteralepas* (Thecostraca, Cirripedia, Thoracica) from the Canary Islands and the

- Azores. Description of mantle ultrastructure.—Zoologicheskii Zhurnal 79(11):1275–1283 (in Russian).
- ——, & M. Y. Schreider. 1992. New species of Cirripedia (Crustacea) from the Indian Ocean.—Zoologicheskii Zhurnal 71(10):39–46 (in Russian).
- Zullo, V. A. 1991. Zoogeography of the shallow-water cirriped fauna of the Galapagos Islands and ad-
- jacent regions in the tropical eastern Pacific. Pp. 173–192 in M. J. James, ed., Galapagos marine invertebrates. Taxonomy, biogeography, and evolution in Darwin's Islands. Plenum Publishing Company, New York, New York.
- —, & W. A. Newman. 1964. Thoracic Cirripedia from a southeast Pacific guyot.—Pacific Science 18(4):355–372.